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The Larval Biology of *Brachidontes modiolus* (Linné, 1767) (Bivalvia : Mytilidae)

by

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Abstract. Larvae of *Brachidontes modiolus* were reared in the laboratory from eggs through to settled juveniles. Egg sizes ranged between 67.3 and 77 μm. Straight-hinge veligers appeared 15 to 17 h after fertilization of the eggs. The length of shelled larvae increased from 96 to 221 μm: the straight-hinge stage from 96 to 176 μm, the umbo stage from 168 to 221 μm, and the pediveliger stage from 180 to 221 μm. Settlement occurred at lengths of 180 μm and upwards. The larval hinge consists of small teeth along the length of the hinge with larger teeth at both ends. Larvae of *B. modiolus* develop more rapidly and settle at an earlier age than larvae of *B. recurvus* and *B. granulata.*

INTRODUCTION

Brachidontes modiolus (Linné, 1767) (=*B. citrinus*) is a small marine mytilid, the adults of which measure between 38 mm (ABBOTT, 1974) and 46 mm (MCLEAN, 1951). The geographic range for this species is from Florida to the West Indies (ABBOTT, 1974). In Barbados, members of this sublittoral species may be found recessed within beds of the seagrass *Thalassia testudinum* Konig or attached to the rocky surface of reef flats at depths of 0–2 m. *Brachidontes modiolus* is highly gregarious and, whether living epifaunally or infaunally, occurs in dense aggregates of individuals.

The specific name *Brachidontes citrinus* (Röding, 1798) has been widely used. ABBOTT (1974), however, considered this to be a synonym of *B. modiolus* (Linné, 1767). Indeed the name 'modiolus' is singularly apt, for *B. modiolus* exhibits characteristics of the *Modiolus* group of mytilids, namely the possession of subterminal umbones and a shell shape which is more conical than triangular (STANLEY, 1970, 1972).

The larval biology of *Brachidontes modiolus* has hitherto been unreported in the literature under any of its synonyms. A knowledge of the duration of the planktonic stage of an aquatic larva, the time during which it is exposed to ocean or coastal currents, could contribute to an understanding of the distribution of a species in a given region. This aspect has been discussed by COE (1953) and SCHELTEMA (1971). In addition, a description of the larval stages of *B. modiolus* would aid in the identification of these larvae when encountered in plankton samples, as well as establish the life history pattern and strategy of the species.

The identification of bivalve larvae has posed problems in the past. LOOSANOFF *et al.* (1966) drew attention to the inadequacy of "indirect methods" of identification of bivalve larvae, and pointed out that these methods have led to discrepancies in the description of larvae of the same species when reported by different authors. Indirect methods include monitoring the development of an unidentified larva found in the plankton through to settling and the assumption of identifiable features of a particular species. These authors recommend "direct methods" of identification, *i.e.*, the rearing of larvae from fertilized egg stage through to metamorphosis under controlled laboratory conditions. The development of reliable methods for obtaining viable gametes and for the rearing of juveniles has resulted in the successful culture of the larvae of several marine bivalves. LOOSANOFF & DAVIS (1963) reviewed methods for the cultivation of larvae and detailed the specific requirements necessary for the successful culture of 19 species of bivalves. As characters to be used in the identification of marine bivalve larvae, LOOSANOFF *et al.* (1966) listed the dimensions of the larval shell (the prodissoconch), its general shape, prominence of the umbones during growth to metamorphosis, and ratios of length of hinge to maximum length or width of shell. CHANLEY & ANDREWS (1971) and CHANLEY & CHANLEY (1980) provided useful terminology for describing larval shell form and, in order to provide a better description of larval shell length, height and depth relationships. LOOSANOFF *et al.* (1966) provided a guide to the dimensions and shapes of

20 species of bivalves, and CHANLEY (1970) gave a review of the larval characteristics of the Mytilidae. Within the genus *Brachidontes*, descriptions of the larvae of *B. recurvus* from the western North Atlantic Ocean have been published in CHANLEY (1970), and of *B. granulata* from central Chile in CAMPOS & RAMORINO (1980). The larvae of *B. senhausi* were described in YOSHIDA (1937), but according to KURODA *et al.* (1971; cited in CAMPOS & RAMORINO, 1980), this species belongs to the genus *Musculus*.

The purpose of this paper is to provide a description of the larval stages of *Brachidontes modiolus*, with information on the development and length of the larval life of the species.

MATERIALS AND METHODS

Gametes were obtained from ripe mussels collected during the peak of the reproductive season (June to September). This peak was determined by continuous sampling and histological techniques over a period of two years. In the laboratory the animals were cleaned of sediment and encrustations and placed in freshly collected sea water. Initially, several methods were employed in an attempt to obtain viable gametes:

(1) temperature shock within the range 24–34°C;
(2) pricking of the posterior adductor muscles of the adults;
(3) introduction of sperm and/or eggs obtained from stripped gonads to water containing ripe mussels;
(4) treatment of stripped gonads with a 0.1 N solution of ammonium hydroxide;
(5) exposing the mussels to hydrogen peroxide in alkaline (pH 9.1) sea water as per MORSE *et al.* (1977). Only this last method was successful; hence, the procedure is detailed below.

Alkaline sea water was prepared with predetermined quantities of Trizma*, hydrochloric acid and natural sea water (pH 7.2). Three or four mussels were placed individually or collectively in beakers containing 50 ml of alkaline sea water per animal (pH 9.1); hydrogen peroxide was then added with a micropipette to a final concentration of 5 mM. This was the treatment solution. The animals were kept in this solution for one hour, after which time the liquid was decanted and replaced with 100 ml of fresh treatment solution. One hour after the second treatment, the mussels were removed from the alkaline sea water, rinsed, and placed in beakers containing 100 ml of natural sea water. These were then placed in a water bath at a temperature of 33–34°C. Males and females received the same treatment. The onset time of spawning varied widely, from 30 minutes to several hours after treatment in the hydrogen peroxide solution. Mussels seen spawning were removed and placed individually in beakers containing natural sea water at 28°C. The eggs were rinsed thoroughly with sea water filtered through glass fiber filter paper. Sperm was added to the egg suspension, and the two allowed to remain undisturbed for 10 min to encourage fertilization. In some instances a female in the process of spawning was placed in a weak sperm suspension, and so the eggs were fertilized as they were extruded. The fertilized eggs were rinsed to remove excess sperm and placed in 150 ml of filtered sea water in Erlenmeyer flasks of 250 ml capacity. Possible contamination of the cultures was reduced by placing tissue paper in the necks of the flasks and covering the opening of the flask with aluminum foil. If flasks containing larvae were left open to the air, a dense population of ciliates soon developed, with consequent death of the larvae. The embryos were left undisturbed for 24 h, at which time the strongly swimming larvae were pipetted off and introduced into fresh sea water to a density of 25–30 larvae/ml. The water containing the larvae thereafter was changed every third day. This was achieved by washing the larvae over a fine nylon mesh which was glued securely over one end of a large open-ended glass tube. Mortality of the larvae during washing was reduced if the mesh was held in a beaker containing filtered sea water, so that the mesh was positioned below the surface of the water. The bottom layer of water in the flask was discarded as dead or weak larvae accumulated there. The flasks were thoroughly washed at each water change, and care was taken to ensure that no detergents contaminated the sea water. The sea water used for each change was freshly collected and filtered. Best survival rates were obtained when the larvae were reared in unaerated sea water.

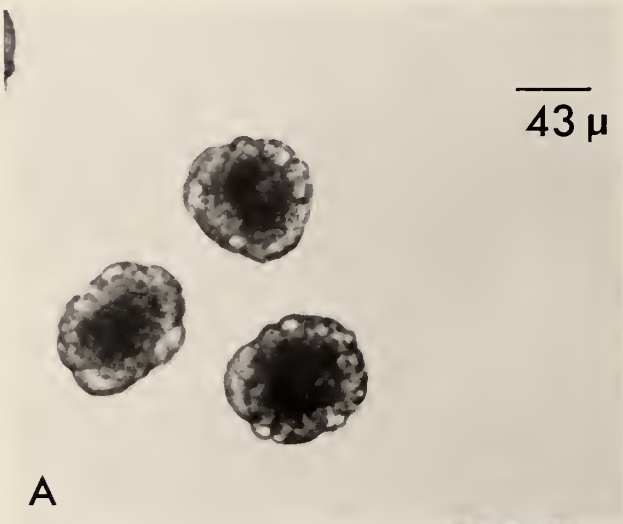
The larvae remained unfed for 48 h and thereafter were fed on a mixture of *Dunaliella tertiolecta* and *Nephroselmis tibron*. When possible, *Isochrysis galbana* was added to the diet. Feeding densities in the case of the larger alga, *i.e.*, *Dunaliella*, was approximately 8000–10,000 cells per ml of culture solution. Concentrations of the smaller alga were higher, 70,000–80,000 per ml of culture solution. Algal concentrations of these magnitudes were cleared by the larvae in 24 h.

Sub-samples of approximately 10 larvae were measured every two days for two weeks. Length was measured as the maximum distance in the antero-posterior direction, height as the maximum distance from the hinge to the ventral margin of the shell, and depth as the maximum left–right dimension (CHANLEY, 1970).

RESULTS

The eggs of *Brachidontes modiolus* ranged in diameter from 67.3–77 μm, and were a uniform dark brown in color. When spawned, the eggs had an irregular appearance but soon became rounded. No measurements were made of the spermatozoa. The sperm obtained from stripped go-

* A brand name. Use here does not necessarily imply endorsement of the product.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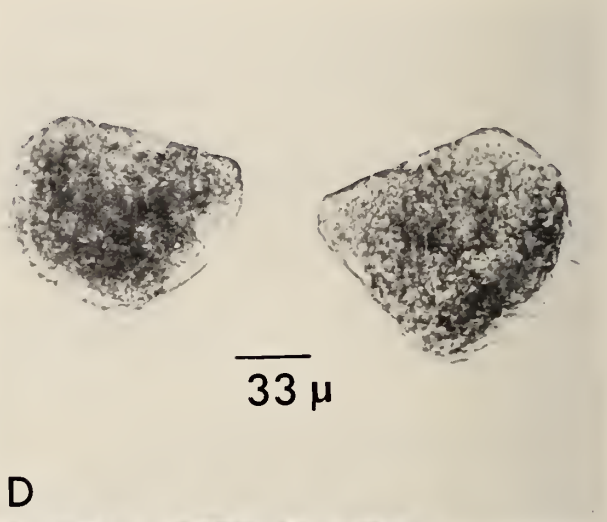
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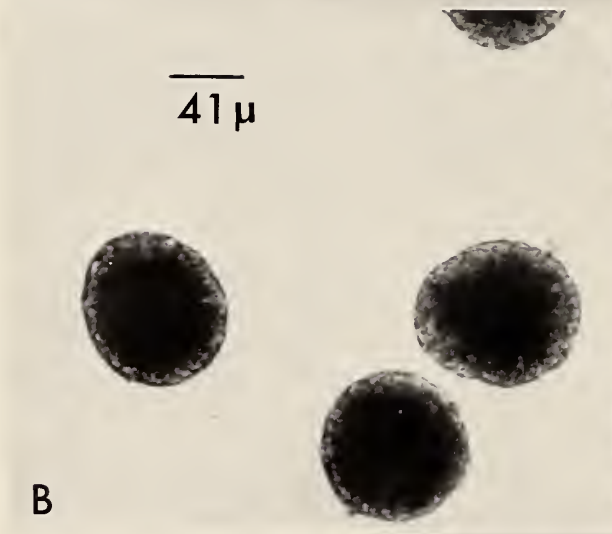
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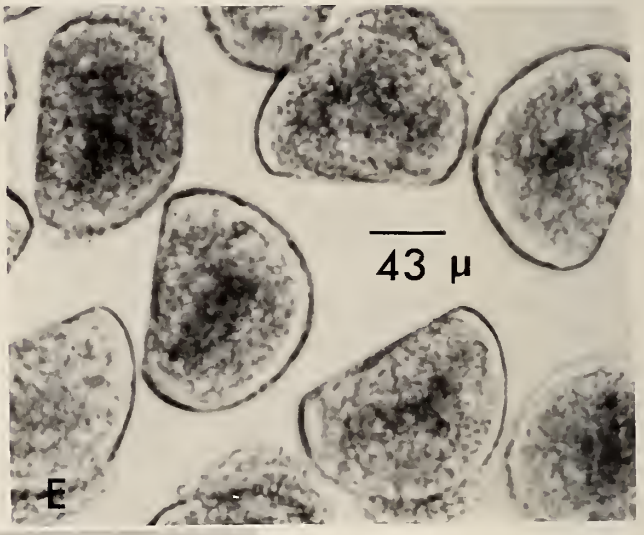
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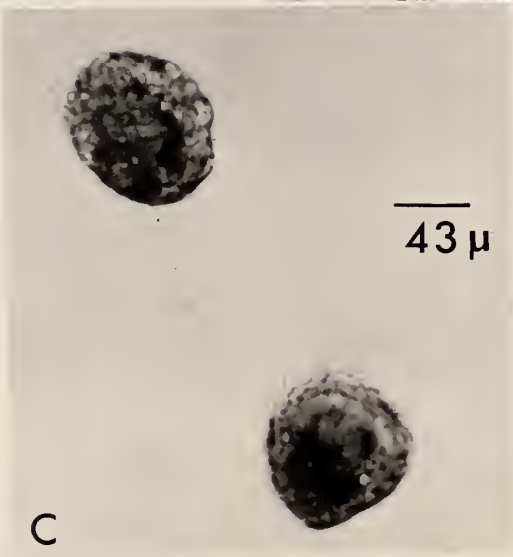
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nads appeared less active than those obtained through the mediation of hydrogen peroxide.

As in BAYNE (1965), the stages chosen to evaluate development times to the straight-hinge stage were those easily recognized and not those with particular embryological significance (Table 1).

Stage 1—First division: the time at which 50% of the sample had undergone first cleavage.

Stage 2—The ciliated blastula: first appearance of cilia, evidenced by slowly rotating larvae (Figure 1a).

Stage 3—The early trochophore: appearance of an apical flagellum (Figure 1b).

Stage 4—Veliger: appearance of long cilia on the apical plate (Figure 1c).

Stage 5—Transitional stage: first appearance of the shell as a transparent object on the dorsal surface of the larva (Figure 1d).

Stage 6—Straight-hinge veliger: the possession of a complete shell, the prodissoconch. Very early straight-hinge veligers are darker than the later ones (Figure 1e).

First division occurred approximately 36 min after fertilization and the ciliated blastula appeared 3 h later. The ciliated blastulae swam slowly at first and as time progressed swam upwards towards the surface of the water column. Development of the trochophore occurred 5 h after fertilization, and veligers were first seen 4 h later. Transitional stages between the veliger and the straight-hinge veliger appeared 12 h from zero time, and straight-hinge veligers were seen in cultures 15–17 h after fertilization. The color of the larvae underwent a change during development, and stages 1 through 5 were dark brown while stage 6, the straight-hinge veliger, was a pale yellow-brown.

The rate of development of the larvae varied with temperature. Larvae reared at 34°C developed into straight-hinge veligers 13 h after fertilization. In cultures kept at 24°C, it was not until 25 h had elapsed that straight-hinge veligers were observed. At the time that straight-hinge veligers were recorded from cultures reared at 28°, 32° and 34°C (*i.e.*, between 13–17 h), larvae reared at 24°C were still at the early trochophore stage.

Larval Dimensions and Shape

The early straight-hinge larvae measure 96 μm in length, with a minimum height of 67 μm. No measurement of depth was recorded at the earliest straight-hinge stage. The smallest depth recorded was 56 μm at a larval length of 152 μm. Straight-hinge larvae attained a size of up to 176 μm in 6 days. Heights then ranged from 126–144 μm, and depths from 84–104 μm. At lengths greater than 176 μm the hinge line invariably showed signs of rounding (Figure 2). Lengths increased faster than height, which in turn increased faster than depth. Between lengths of 96 and 115 μm, heights were 19–29 μm less than length, while at a length of 176 μm, heights measured 32–50 μm less than length. The first indication of umbo development appeared at 168 μm, with heights ranging from 120–136 μm and depths from 72–88 μm. All observed combinations of larval heights and depths for a given length are given in Figure 3. The length of the hinge at a shell length of 152 μm was 120 μm, increasing to 128 μm at a shell length of 168 μm. The results are summarized in Table 2 and Figure 2.

The straight-hinge larva is roughly "D" shaped. The hinge line is long relative to the length of the shell. The shoulders slope steeply, with the posterior shoulder shorter and sloping more steeply than the anterior. The posterior end is higher and more pointed than the anterior. The ventral margin of the shell is rounded. The hinge line becomes slightly rounded with the development of the umbo, and is at first "round" or "indistinct." The umbo may remain low and not clearly defined through lengths of 168–288 μm, becoming "broadly rounded" in later stages. The minimum length at which the umbo was seen to project above the shell margin is 240 μm. The shoulders at this stage are almost straight, the anterior shoulder not sloping as steeply as the posterior. The ventral margin is now markedly elongate, but still rounded. The larval hinge consists of a series of small teeth, flanked by two or three larger teeth.

Table 1

Summary of the observed development times of the larvae of *Brachidontes modiolus*. Temperature = 28°C.

Stage	Description	Time
0	Fertilization	0
1	First division	34–36 min
2	Ciliated blastula	3 h 40 min
3	Early trochophore	5 h 15 min
4	Veliger	9 h 15 min
5	Transitional stage	12 h
6	Straight-hinge veliger	15–17 h

←

Figure 1

Stages in the early larval development of *Brachidontes modiolus*. A. ciliated blastula; B. early trochophore; C. veliger; D. transitional stage; E. straight-hinge stage.

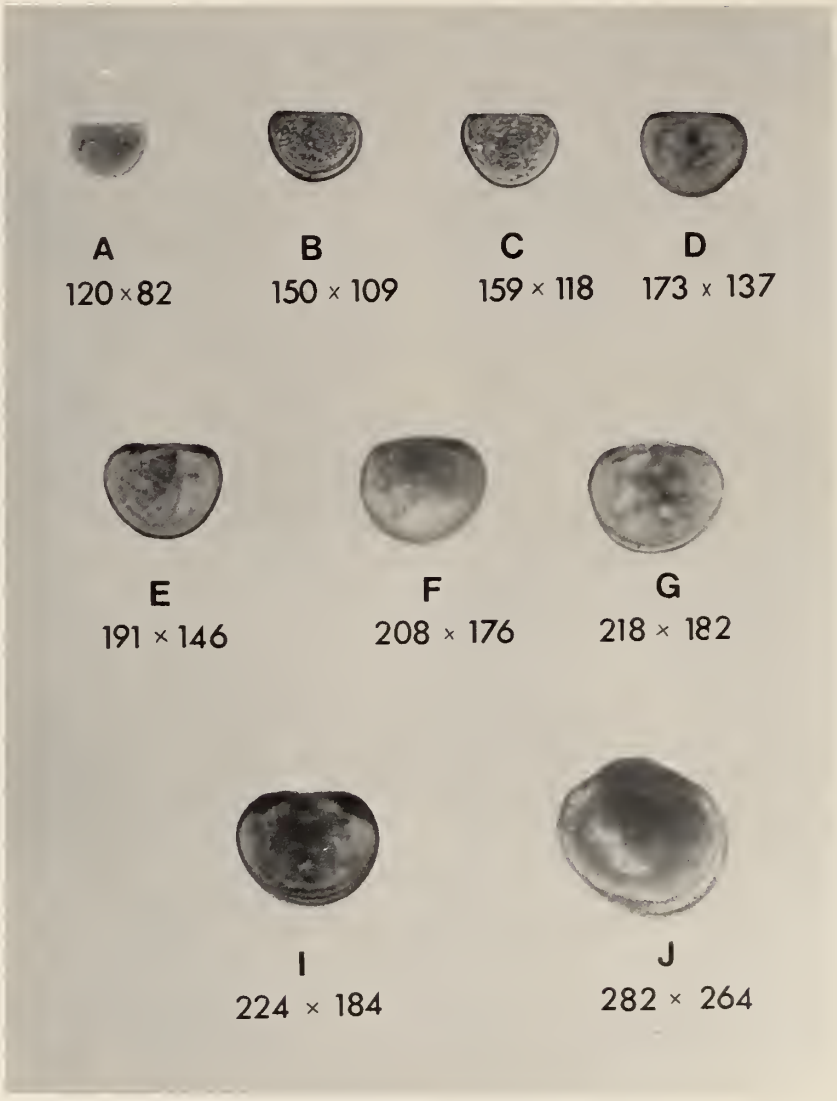

Figure 2

The larvae of *Brachidontes modiolus* at different stages of development from the early straight-hinge stage (A) to settlement (G–I). Larvae are positioned with anterior end to the left, except in J. The larva in J is an early juvenile just beginning dissoconch growth. The length and height of the larvae are indicated under each photograph; measurements are in microns.

The smallest pediveliger larva seen using its foot measured 180 μm (Figure 4) in length, but more generally, ambulatory pediveligers appeared at a length of 184 μm. The eye spot first appeared in larvae at length 184 μm when cultured at temperatures of 32° and 34°C.

Internal Anatomy of the Larvae

The internal anatomy of the larva was at first indistinct at magnifications of up to 500×. The gut became apparent on the first day as a straight tube running in a posterior direction. It soon became coiled (Figure 5a). The digestive gland soon became easily visible, as with the onset of feeding in the larvae, the organ developed a green-brown color (Figure 5b). The adductor muscles showed clearly by the third day, and the velar retractor muscles were also conspicuous at this time. The foot was fully developed by day 6, with the pedal retractor muscles clearly visible (Figure 5c, d). The velum increased in size with the development of the larva to the pediveliger stage, and occupied a large portion of the shell cavity. The gill filaments were not clearly visible until after metamorphosis (Figure 5e). The

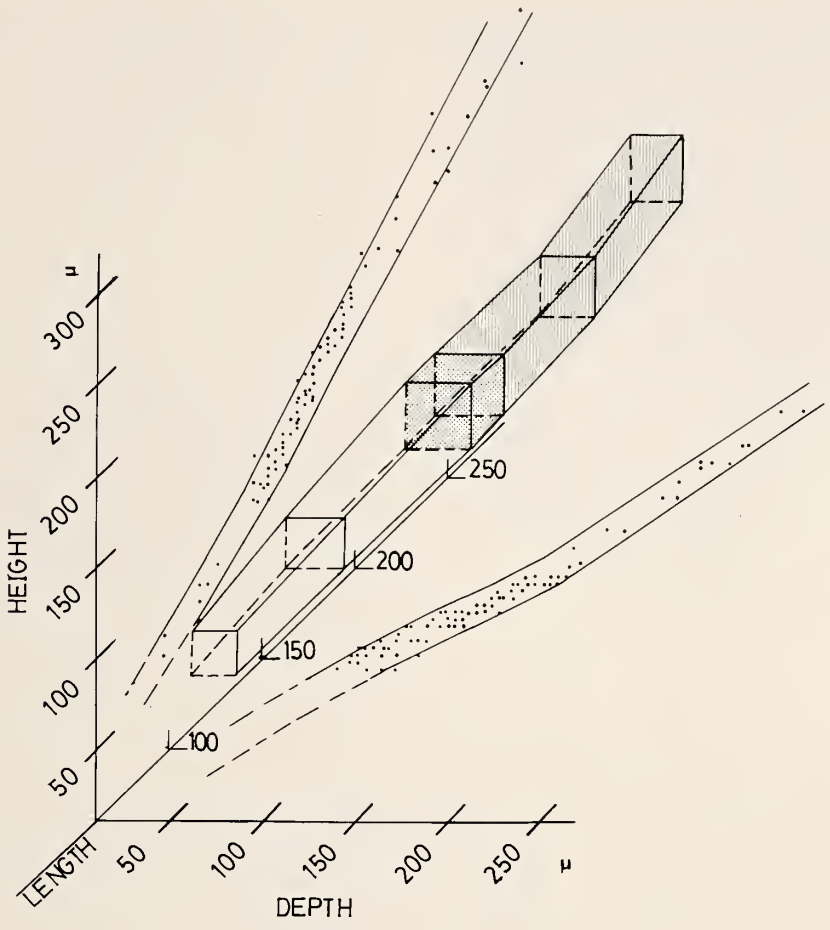

Figure 3

Larval dimensions of *Brachidontes modiolus*. The height and depth co-ordinates run parallel to the length axis. The dots represent length-depth or length-height measurements. The lines enclosing the dots were fitted by eye and represent maximum and minimum height and depth measurements. The three-dimensional figure represents all possible length, height, and depth combinations for *B. modiolus* (after CHANLEY & VAN ENGEL, 1969). The clear area represents the straight-hinge stage, the lined area the umbo stages, and the stippled area, the transitional stage between straight-hinge and umbo forms.

larvae of *Brachidontes modiolus* settled at sizes between 180 and 221 μm in length and settlement occurred from day 11 onward, although swimming larvae were still visible in the medium up to the 30th day.

DISCUSSION

Induction of Spawning

LOOSANOFF & DAVIS (1963) list methods used in the induction of spawning in 19 bivalves. They pointed out that where some species responded to thermofluctuation as a stimulus to spawning, others needed the additional stimulus of a sperm or egg suspension. In some instances special methods had to be employed, such as pricking the

Table 2

Summary of larval dimensions of *Brachidontes modiolus*.

Stage	Length (μm)	Height (μm)	Depth (μm)
Early straight-hinge stage	96	76	*
Straight-hinge stage	96–176	67–152	*–100
First indication of umbo	168	120–136	72–88
Umbo stage	168–221	120–184	72–124

* Not measured.

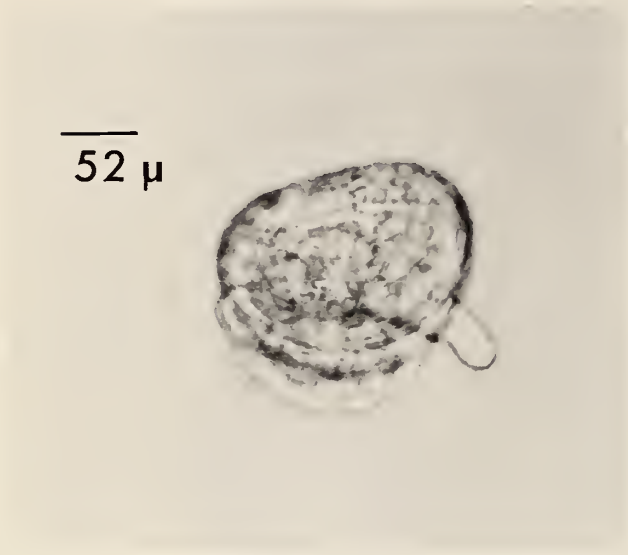

Figure 4

Pediveliger of *Brachidontes modiolus*.

adductor muscle in *Mytilus edulis*. Other species, like *Modiolus demissus*, did not respond to any treatment; Loosanoff & Davis (1963) were unsuccessful in inducing this species to spawn. Wilson & Hodgkin (1967) failed to induce spawning of *Brachidontes cf. variabilis* in the laboratory. Chanley (1970) was finally successful in causing spawning in *B. recurvus* by placing the mussels in sea water with temperatures fluctuating between 20 and 32°C. Previous attempts to induce spawning in this animal, by adding stripped gametes to the water or stretching or injuring the adductor muscles, had proved unsuccessful. Ripe adults of *B. granulata* spawned when placed in filtered sea water at 16°C after being held in an incubator at 6°C for 12 h. The account presented above demonstrates the individuality of the response of different species to various spawning stimuli.

Stripping of the gonad of *Brachidontes modiolus* failed to produce viable gametes for the same reason that the eggs obtained through the mediation of 0.5 M KCl are not fertilizable. Raven (1958) stated that maturation of the eggs of most mollusks may begin spontaneously, independent of fertilization, *e.g.*, after spawning in sea water, and continues until metaphase of the first maturation division. Unfertilized eggs are blocked at this stage. Maturation is evidenced in part by the dissolution of the germinal vesicle. The ova of *B. modiolus* are not mature while still in the gonad. Eggs from this species, when obtained by stripping or by injection of KCl, possessed an intact germinal vesicle and were therefore immature and were incapable of being fertilized without further treatment (*e.g.*, the addition of NH_4OH). In contrast, the eggs extruded from mussels stimulated by the addition of hydrogen peroxide had started the maturation process and were easily fertilizable.

Morse *et al.* (1977) found that the hydrogen peroxide-induced spawning of the abalone *Haliotis rufescens* may have resulted from a "direct activation of the enzyme-catalyzed synthesis of prostaglandin endoperoxide." Prostaglandin endoperoxide (PGEP) is produced from arachidonic acid through a series of reactions, the first step of which is catalyzed by the enzyme fatty acid cyclooxygenase (=PGEP synthetase). These investigators showed that abalone eggs and gonads from ripe animals of both sexes contained large quantities of cyclooxygenase, and further that hydrogen peroxide directly increased the rate of the reaction catalyzed by the PGEP-forming cyclooxygenase from reproductive cells of the abalone. PGEP synthetase has been implicated in the control of spawning not only in abalones, but in *Mytilus californianus* (Morse *et al.*, 1977) and sea urchins (Morse *et al.*, 1978). It is probable that a similar control of spawning exists in *Brachidontes modiolus*. Iwata (1952) found that electrical stimulation induced maturation of eggs of *Mytilus edulis*. He suggested that the stimulus was mediated by the ovary, probably by the secretion of some substance that caused the ova to mature. According to Iwata (1952), spawning in *Mytilus* appeared to follow automatically as soon as the eggs begin the maturation division, and therefore spawning in this animal depended entirely on whether the maturation process had taken place. A number of questions arise from a comparison of the results of Morse *et al.* (1977) and Iwata (1952). Could the proposed substance of Iwata (1952) be related to PGEP synthetase, or to any of the enzymes or intermediate products of PGEP production? Conversely, does PGEP synthetase act to promote maturation of oocytes and hence spawning?

The role of PGEP synthetase in the control of spawning in *Brachidontes modiolus* would be of interest for further study. Morse *et al.* (1977) stated that the fatty acid-cyclooxygenase reaction may be potentially rate-limiting in the physiological sequence of reactions leading to spawning and therefore possibly under hormonal and/or neural control. Thus a knowledge of the levels of this enzyme in *B. modiolus*, together with information on environmental factors, could help in determining the ultimate factors controlling the release of gametes in this species.

Larval Survival and Development

Larvae survived well in unaerated cultures, and change of water every third day proved adequate for removing toxic waste products before harmful levels were reached. Some morphological malformations were observed in some of the larvae, for example concavity of the hinge line or un-equal valve growth; but it could not be determined to what extent these were due to culture conditions. Abnormality of the hinge line as seen in *Brachidontes modiolus* was also reported for other bivalves (Loosanoff & Davis, 1963). In addition, these authors described another type

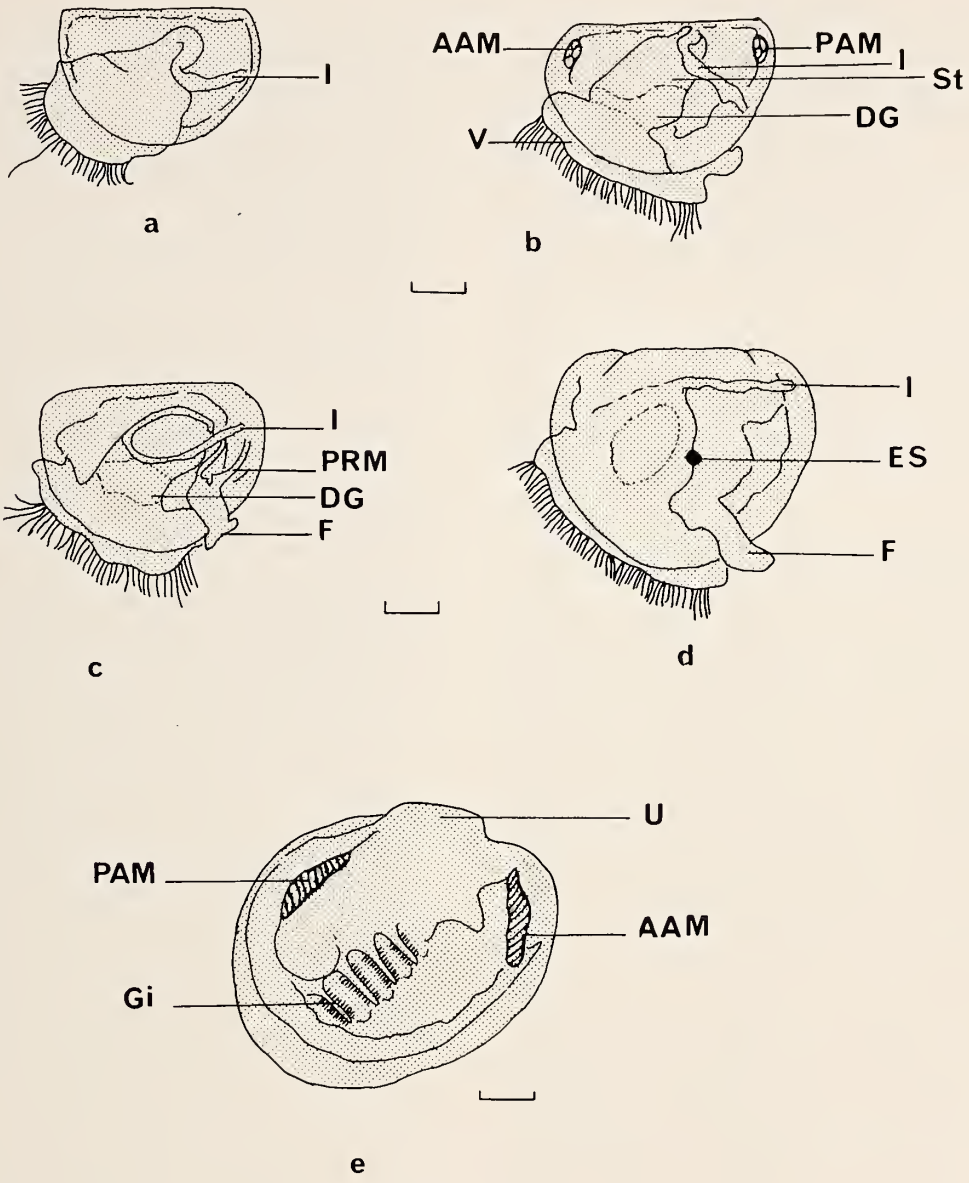

Figure 5

Diagrams of conspicuous features of the internal anatomy of *Brachidontes modiolus*. a. straight-hinge veliger; b. 3-day old larva; c and d. 6-day old larvae; e. spat. Scale bar for a, b, c, and d is 40 μm long; for e, it is 60 μm long. AAM, anterior adductor muscle; DG, digestive gland; ES, eye spot; F, foot; Gi, gills; I, intestine; PAM, posterior adductor muscle; PRM, pedal retractor muscle; St, stomach; U, umbo; V, velum.

of larval abnormality in which there was no clear-cut anatomical malformation, but rather the larvae were unable to feed. Such larvae developed to the straight-hinge stage but grew no further and eventually died. It is probable that the larvae found in the bottom layers of cultures of *B. modiolus* suffered from this type of "feeding" abnormality. Loosanoff & Davis (1963) reported that this type of abnormality in *Mercenaria mercenaria* was related in some instances to the type of food fed to the larvae. This aspect was not investigated in *B. modiolus*.

That larvae of various species of bivalves show variation in growth rate among individuals reared from the same spawn under similar conditions is well established (Loosanoff & Davis, 1963). In addition to individual variation in growth rate, larvae of *Brachidontes modiolus* settle at different times after 11 days. Loosanoff & Davis

Table 3

Summary of the major features of the larvae of *Brachidontes modiolus, B. recurvus**, and *B. granulata***.

Stage or distinctive feature	Size (μm)		
	B. modiolus	*B. recurvus*	*B. granulata*
Unfertilized egg	67–77	62–68	63–73
Straight-hinge veliger	96–176	90–165	177†
Appearance of umbo	168	135	150
Conspicuous eye spot	184	180	—
Pediveliger (first appearance of functional foot)	180	165	200

* Data taken from CHANLEY (1970).
** Data taken from CAMPOS & RAMORINO (1980).
† Length of prodissoconch.

(1963) found that the number of days needed for larvae of the same cultures to reach settling stage was not sharply defined, even for a culture reared under standard well-controlled conditions. The observed extended settling period of *B. modiolus* may be explained by the probability that glass is not the most desirable substrate for settling, as well as it may be related to factors governing settling density. Larvae possessing a functional velum could be seen swimming in the water column long after others in the same flask had settled and attached themselves by byssal threads. BAYNE (1965) discussed the delay of metamorphosis in *Mytilus edulis* and showed that the larvae become capable of attachment and metamorphosis some time before they would attach to glass, and that the majority died without attachment. The delay of metamorphosis of laboratory reared larvae has been previously reported for other bivalves: CULLINEY (1971) for *Lithophaga bisulcata,* CAMPOS & RAMORINO (1980) for *Brachidontes granulata.* BAYNE (1965) established that the larvae of *Mytilus edulis* settled preferentially on filamentous algae (primary settlement). The larvae of *B. modiolus* did not settle on algae provided in the culture flasks. However, in another experiment not described here, a fine filament of artificial fiber of unknown origin precipitated mass gregarious settlement of larvae of *B. modiolus.* In the wild population no sign of attachment to algae by the larvae of *B. modiolus* was recorded in this study.

CHANLEY (1970) described the common characteristics of larval Mytilidae. The larvae of *Brachidontes modiolus* exhibited many of the features listed. The hinge line was long in relation to larval length and increased in size with growth of the larvae. The hinge possessed a mytilid dentition, having a series of small teeth along the length of the hinge, with larger teeth towards the end. The umbo was late in developing and remained indistinct. In fact, it was not until after settling that the umbo of *B. modiolus* became pronounced. However, the larvae of *B. modiolus* set at a smaller size (180–221 μm) than most mytilid larvae (300 μm, in CHANLEY, 1970) as do larvae of other species of this genus (Table 3).

A comparison of the development of the larvae of *Brachidontes modiolus, B. recurvus,* and *B. granulata* (Table 3) reveals differences in size at first appearance of the umbo and in minimum sizes of the pediveligers. The shape of the straight-hinge veliger of *B. modiolus* more closely resembles that of *B. recurvus* than that of *B. granulata.* The shape of this larval stage of *B. granulata* is more rounded than that of the former two. If, however, a comparison is made of later stages, the position is reversed, with the larvae of *B. granulata* being more similar in shape to that of *B. modiolus* than *B. recurvus.* The most notable difference is in the developmental times of the three species. Pediveligers first appeared after 6 days and settlement of the larvae of *B. modiolus* occurred from the 11th day onwards, similar to the time of the first appearance of pediveligers of *B. recurvus.* CHANLEY (1970) does not report on the time of settlement of *B. recurvus.* The pediveligers of *B. granulata* do not appear until 55 days after fertilization, and CAMPOS & RAMORINO (1980) report no evidence of metamorphosis up to 33 days after this. This lack of metamorphosis in the larvae of *B. granulata* was attributed to the unavailability of a substrate suitable for settlement of the pediveligers. The variation in the developmental times may result from the different temperature regimes to which the larvae were exposed. The larvae of *B. granulata* were reared at 12–16°C, those of *B. recurvus* at 25°C, and the larvae of *B. modiolus* at 28°C. BAYNE (1976) presented data from various authors on the rates of cleavage and early development of *Mytilus edulis* at different temperatures (8–22°C). Those results showed that development proceeded more rapidly at the higher temperatures.

In general the developmental progress and morphology of the larvae of *B. modiolus* closely resemble those of the larvae of the other two members of the genus *Brachidontes* described in the literature. In the early stages the larvae of *B. modiolus* bear strongest resemblance to those of *B. recurvus* while at later stages the more obvious resemblance is to the larvae of *B. granulata.* These findings tend to reinforce the family or group relationships of these three species. The most outstanding difference is in the developmental times, with *B. modiolus* settling the earliest of the three.

This difference has been attributed to different temperature regimes at which the larvae were reared. *Brachidontes recurvus* was reared at 25°C, *B. granulata* at temperatures between 12° and 16°C, and *B. modiolus* at 28°C.

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